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Reconstructing the History of Marriage Strategies in Indo-European–Speaking Societies: Monogamy and Polygyny

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Keywords

INDO-EUROPEAN, CULTURAL PHYLOGENETICS, MARRIAGE, MONOGAMY, POLYGyny

Cover Page Footnote

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Reconstructing the History of Marriage Strategies in Indo-European-Speaking Societies: Monogamy and Polygyny

LAURA FORTUNATO¹

Abstract Explanations for the emergence of monogamous marriage have focused on the cross-cultural distribution of marriage strategies, thus failing to account for their history. In this paper I reconstruct the pattern of change in marriage strategies in the history of societies speaking Indo-European languages, using cross-cultural data in the systematic and explicitly historical framework afforded by the phylogenetic comparative approach.

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Introduction

Background. Explanations for monogamous marriage have centered around the prevalence of this practice in Eurasia (Holy 1996, pp. 62–63), linking its emergence to the development of idiosyncratic features of societies in the region. These include, for example, the establishment of large nation states (e.g., Alexander 1987) and democracy (e.g., Fox 1997); the spread of Christianity (e.g., Goody 1983, 2000); the onset of industrialization and urbanization (e.g., Betzig 1982, 1986; van den Berghe and Barash 1977), and of economic development more generally (e.g., Gould et al. 2008). Consistently, cross-cultural analyses show that societies scoring high on scales measuring “societal complexity” tend toward monogamous marriage (Levinson and Malone 1980, p. 37; e.g., Blumberg and Winch 1972; Lee 1979; McNett 1973; Osmond 1965, 1969; Sheils 1971).

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KEY WORDS: INDO-EUROPEAN, CULTURAL PHYLOGENETICS, MARRIAGE, MONOGAMY, POLYGyny.

By focusing on the cross-cultural distribution of marriage strategies, these studies fail to account for their history. Restrictions on polygynous marriage appear in the earliest historical records, long predating the development of aspects of social organization typically associated with Eurasian societies and with “societal complexity” and “modernization” more generally (see review in Scheidel 2009 and discussion in Fortunato and Archetti 2010). In this paper I reconstruct the pattern of change in marriage strategies in the history of societies speaking Indo-European (IE) languages, using cross-cultural data in the systematic and explicitly historical framework afforded by the phylogenetic comparative approach (Mace and Pagel 1994; e.g., Fortunato et al. 2006; Fortunato and Jordan 2010; Jordan et al. 2009). In the companion paper I extend this framework to reconstructing the history of residence strategies in the same set of societies (Fortunato 2011). Finally, this framework is extended in Fortunato (2009) to investigate the co-evolution of monogamous marriage and neolocal residence; on this analysis, it cannot be excluded that the observed association between marriage and residence strategies is the artifact of a history of descent of these societies from a common ancestor.

Phylogenetic tree-building analyses of linguistic data support Renfrew’s (1987) hypothesis for the origin of the IE language family, which envisages an expansion from Anatolia with the spread of agriculture starting between 7000 and 6000 BCE (Gray and Atkinson 2003; see also Atkinson et al. 2005; Atkinson and Gray 2006a,b). This scenario involves an early split of IE languages from their sister group, the extinct Anatolian family, which comprises the extinct languages Hittite, Palaic, Lydian, Luwian, and Lycian; together, IE and Anatolian form the Indo-Hittite language family (Ruhlen 1991, pp. 325–327). The other main competing hypothesis, proposed by Gimbutas (1973a,b), places the homeland of the language family in the Pontic steppes north of the Black Sea and posits an expansion driven by nomadic horse-riding pastoralists starting after 4000 BCE (Diamond and Bellwood 2003). Consistent with the former scenario, I use the terms “Proto-Indo-European” (PIE) for the hypothetical ancestor of IE languages and “Proto-Indo-Hittite” (PIH) for the hypothetical ancestor of Indo-Hittite languages, as well as for the hypothetical “proto-societies” that spoke them. Other classifications, based on alternative explanations for the origin of the IE language family, use PIE for the ancestor of IE and Anatolian languages (i.e., they classify Anatolian languages as IE; e.g., Mallory and Adams 2006). To avoid confusion, throughout this and the companion paper I have changed instances of the latter usage to the one stated here.

Related Research. Early IE marriage strategies have been reconstructed on the basis of linguistic and ethnographic evidence. The linguistic evidence is, at best, tenuous. The correspondence of the Middle Irish (Celtic sub-group, c. 900–1200 CE) and Avestan (Iranian sub-group, first millennium BCE) terms for “concubine, wanton woman” suggests that PIH society recognized some form of polygynous mating, if not polygynous marriage; this interpretation is supported

by the use of specialized terms to designate legitimate children (Huld and Mallory 1997, p. 123). A second line of evidence relates to the concept of widowhood: while it is possible to reconstruct a PIH term for “widow,” there is no corresponding term for “widower.” One interpretation of this pattern is that male widowhood was not recognized in PIH society because men married polygynously, such that the death of one wife did not affect their marital status (Huld 1997, p. 642). Implicit in this interpretation are, however, a number of unrealistic assumptions, for example that *all* PIH men married multiple wives and that they rarely, if ever, outlived their wives; both represent demographic impossibilities.

Based on the ethnographic evidence, Murdock (1949, p. 349) reconstructed “an Eskimo type of social structure in the prehistory of the Indo-European peoples.” The defining features of this type of social organization are the presence of the Eskimo system of cousin terminology and the absence of exogamous unilineal kin groups; additional typical characteristics include the presence of monogamy, independent nuclear families, and neolocality, but variant sub-types characterized by non-neolocal marital residence may feature polygyny and extended families (Murdock 1949, p. 227). In the Eskimo type of cousin terminology all cousins are equated with each other but differentiated from siblings; unilineality refers to kin groups organized around principles of matri- or patrilineal descent; neolocality indicates residence of married couples apart from the kin of either spouse. The reconstruction was inferred from the social organization of five societies speaking IE languages, representing four of the major sub-groups of the language family. Specifically, the social systems of Yankees (Germanic sub-group) and Ruthenians (Slavic sub-group) are of the Eskimo type, the social systems of Albanians (Albanian sub-group) and Ossets (Indo-Iranian sub-group) include features suggesting “Eskimo antecedents,” while the social system of the Kurds (Indo-Iranian sub-group) is not incompatible with the Eskimo type. Quite apart from the small number of societies upon which the reconstruction was based, Murdock’s (1949) approach presents a serious methodological issue. According to Fox (1967, p. 262), modern IE terminologies for kin and affines (in-laws) tend to show a much stronger bias toward the nuclear family than was the case for early IE terminological systems. This brings into question the validity of inferences about past social organization drawn from kinship and affinal terminologies (see the companion paper).

Finally, Fortunato and Mace (2009) used the ethnographic evidence in a phylogenetic comparative framework to test the hypothesis of co-evolution of bridewealth with polygyny (Hartung 1982) and of dowry with monogamy (Gaulin and Boster 1990) in a sample of 51 societies speaking IE languages. This analysis reconstructed monogamy with dowry as the most likely state at the root of a phylogenetic tree representing the historical relationships among the 51 societies; in addition, the tree included Hittite, thus the root of the tree corresponded to PIH. The reconstruction was obtained using the maximum-likelihood phylogenetic comparative method developed by Pagel (1994) and

implemented in Discrete (Pagel n.d.); this method estimates the evolutionary scenario that is most likely to have produced the observed distribution of states of the two traits across taxa at the tips of the tree. The tree was generated through phylogenetic tree-building analysis of the corresponding 51 speech varieties in Dyen et al.'s (1992) IE basic vocabulary database, using a maximum-parsimony optimality criterion, as implemented in PAUP* 4.0b4a (Swofford 2002); this approach finds the tree or set of trees that optimizes the degree of fit to the data. However, the use of a “best” tree for phylogenetic comparative analysis is problematic, because results are affected by the topology and other parameters (e.g., branch lengths) of the tree used (e.g., Martins and Housworth 2002; see discussion in Fortunato 2008). Thus, while controlling for the effect of descent on the distribution of cultural practices, Fortunato and Mace's (2009) reconstruction may be contingent upon the phylogenetic tree model used to represent how the societies are related.

Rationale and Objective. For the most part, previous attempts to infer early IE marriage strategies from linguistic and ethnographic data have failed to use a systematic and explicitly historical approach. Where such an approach has been taken, the available methods did not account for uncertainty in the phylogenetic tree model used to represent population history.

Here I use a phylogenetic comparative method, in a Bayesian reversible jump (RJ) Markov chain Monte Carlo (MCMC) framework, to reconstruct the pattern of change in marriage strategies in the history of societies speaking IE languages. Using a phylogenetic tree to represent how the taxa are related, phylogenetic comparative methods infer likely evolutionary scenarios that produced the observed distribution of the attribute(s) of interest across the taxa. The Bayesian MCMC framework uses a single tree or a sample of trees to represent the relationships among the taxa; use of a tree sample removes dependence of the inferences upon any single phylogenetic hypothesis. This is particularly important for application of the phylogenetic approach to cross-cultural data, because the reticulate nature of the interactions linking human societies cannot be captured by any single tree model (see discussion in Bellwood 1996). In a similar way, the RJ-MCMC implementation of the approach removes dependence of the inferences upon any single model of trait evolution; the model of trait evolution specifies, for example, whether a trait is likely to be acquired and lost at the same or at different rates. This is also crucial in the analysis of cultural traits, because the mechanisms of change are usually unknown for these traits. More generally, the Bayesian MCMC framework estimates the degree of statistical uncertainty in the parameters of interest to the comparative question (e.g., in the rates of trait change); this provides an indication of the degree of confidence that can be placed in any particular inference about the evolution of the trait(s). A non-technical introduction to the approach is presented in Fortunato (2008).

Phylogenetic comparative methods assume that traits are transmitted vertically (i.e., from parent to daughter populations, along the branches of the phylogenetic tree model used to represent how the taxa are related); consequently, high rates of horizontal transmission of traits across societies may invalidate their application to cross-cultural data (Borgerhoff Mulder 2001; Borgerhoff Mulder et al. 2006; Nunn et al. 2006; Rogers and Cashdan 1997). Recent simulation analyses show, however, that phylogenetic comparative methods outperform non-phylogenetic methods under a wide range of simulated scenarios and levels of horizontal transmission (Currie et al. 2010; Nunn et al. 2006). In any case, kinship and marriage systems appear to be “conservative” features of social organization (Murdock 1949, p. 196); in the context of linguistic and genetic variation, the effect of descent (i.e., vertical transmission) is strongest at the supra-regional level, while the effect of contact (i.e., horizontal transmission) prevails within regions (Borgerhoff Mulder et al. 2001, 2006; Burton et al. 1996; Guglielmino et al. 1995; Hewlett et al. 2002; Holden and Mace 1999; Jones 2003; Moylan et al. 2006). This makes traits relating to kinship and marriage systems especially suited for analysis within the phylogenetic comparative framework.

Data and Methods

I used data on marriage strategy from the *Ethnographic Atlas* (*EA*) (Gray 1999; Murdock 1967) for a sample of societies speaking IE languages. The cross-cultural data were mapped onto a sample of trees representing how the societies are related, obtained by Pagel et al. (2007) through tree-building analysis of Dyen et al.’s (1992) IE basic vocabulary database. Finally, on the cross-cultural data and tree sample I used the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) to reconstruct ancestral states of marriage strategy.

Cross-Cultural Data. The *EA* is distributed in electronic form through the *World Cultures* journal. Variable identifiers in this section follow Gray’s (1999) *EA* codebook. The data in binary form are in the supporting information (SI) file; a map of their geographical distribution is in Figure 1. The cross-cultural sample was collated by matching societies in the *EA* with speech varieties in Dyen et al.’s (1992) IE basic vocabulary database, as described in the SI file.

I coded societies included in the cross-cultural sample as monogamous (state M) or polygynous (state P) based on *EA* variable 9, which scores societies on the prevailing form of family organization (after Murdock 1962). I collapsed the five categories for polygynous marriage, thus ignoring the distinction between limited and general polygyny, between general polygyny with sororal and non-sororal co-wives, and between general polygyny with co-wives occupying the same or distinct dwellings. This produced a sample with 18 (66.7%) of 27 societies coded as monogamous and 9 (33.3%) coded as polygynous (Figure 1 and SI Table 1).

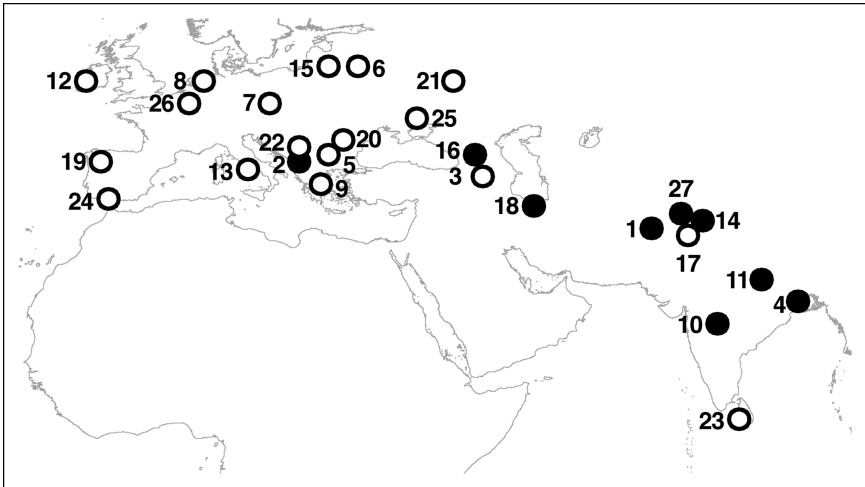


Figure 1. Map illustrating the geographic distribution of the recoded *EA* data in Table 1 in the SI file. Colors express the marriage strategy (white, M; black, P), as per Figure 4; numbers correspond to taxa in Figure 4 and to entries in the relevant column in Table 1 in the SI file.

Tree Sample. I used Pagel et al.’s (2007) posterior probability sample of 750 phylogenetic trees to represent how societies in the cross-cultural sample are related by way of descent from a common ancestor. Trees are present in the sample in proportion to their posterior probability, which is the probability of the tree conditional on the data and model of word evolution used in the tree-building analysis, and can be interpreted as the probability that the tree is correct (Huelsenbeck et al. 2001). For example, the Ibero-Romance speech varieties included in the tree-building analysis by Pagel et al. (2007) (Brazilian, Catalan, Portuguese ST, and Spanish) share an ancestor in 84% of the trees in the sample; the probability that they are a “monophyletic” group is thus 0.84, given the data and model of word evolution used in the tree-building analysis. As discussed below, use of a tree sample instead of a single “best” tree amounts to incorporating phylogenetic uncertainty in the comparative analysis; the degree of phylogenetic uncertainty at several of the nodes in the Pagel et al. (2007) tree sample emphasizes the importance of doing so in this case (Figure 4).

Pagel et al. (2007) inferred the posterior probability distribution of trees from Dyen et al.’s (1992) IE basic vocabulary database, using the Bayesian MCMC phylogenetic tree-building method developed by Pagel and Meade (2004), as described in the SI file. I obtained the tree sample from Mark Pagel. I pruned the trees to retain only the speech varieties corresponding to the 27 societies in the cross-cultural sample, plus the outgroup Hittite, using Andrew Meade’s program BayesTrees (Figure 4). “Outgroup” taxa provide information on the direction of change in the data by virtue of being distantly related to the groups under investigation, the “ingroup” taxa; they are used in tree-building for

determining ancestor-descendant relationships (Felsenstein 2004, p. 6). I preferred this “pruning” strategy, over the alternative of generating a tree sample for the speech varieties included in the comparative analysis (e.g., Fortunato et al. 2006), because the accuracy of phylogenetic tree-building grows with increased sampling of taxa (e.g., Zwickl and Hillis 2002). Hittite was retained for consistency with previous work (Fortunato et al. 2006; Fortunato and Mace 2009) but was assigned no marriage strategy data for the purpose of the comparative analysis.

Comparative Analysis. Reconstruction of ancestral states using the phylogenetic comparative method developed by Pagel and colleagues (Pagel and Meade 2005, 2006; Pagel et al. 2004) is performed using BayesMultistate, available as part of the BayesTraits package (Pagel and Meade n.d.) from <http://www.evolution.rdg.ac.uk/BayesTraits.html>. Unless otherwise specified, the information in this section is based on Pagel and Meade (2005, 2006), Pagel et al. (2004), and on the BayesTraits manual (Pagel and Meade n.d.), to which I refer the reader for a more detailed description of the method and its application. A non-technical discussion of the method is in the SI file.

Given the cross-cultural data and tree sample, BayesMultistate uses parameters q_{MP} and q_{PM} to describe the evolution of the trait “marriage strategy” on a tree. q_{MP} and q_{PM} measure the instantaneous rates of change, respectively, from monogamy to polygyny (i.e., from state M to state P) and from polygyny to monogamy (i.e., from state P to state M); they are used to define the probabilities of these changes, the probabilities of the two states at internal nodes on the tree, and the likelihood of the data, which is the probability of the data given the tree and the model of trait evolution specified by the rates (Pagel 1994, 1997, 1999). In the likelihood calculations BayesMultistate treats taxa that are not assigned comparative data, like the outgroup Hittite in this case, as taking any state with equal probability.

In Bayesian RJ-MCMC mode, BayesMultistate uses RJ-MCMC methods to estimate the posterior probability distributions of rate parameters and of ancestral states at internal nodes on a tree, and of the possible models of trait evolution specified by the rate parameters (see the SI file for details). Four model categories are possible in this case: that q_{MP} and q_{PM} take distinct positive values, that they take the same positive value, or that either one is set to zero while the other takes a positive value. The posterior probability of a parameter value is a quantity proportional to its likelihood of having produced the observed data and represents the probability of the parameter value given the data and model of trait evolution. Schematically, the posterior probability distributions are estimated by running RJ-MCMC chains that sample states in the model of trait evolution in proportion to their posterior probability, across trees in the tree sample; a state in the model consists of model category and values of the rate parameters and ancestral state probabilities. Combining estimates over the sample produced by a chain amounts to “averaging” inferences over uncertainty in the phylogeny, in the parameters of the model of trait evolution, and in the model itself.

I performed five sets of analyses, each comprising five separate chains started from random seeds. One set estimated the posterior probability distributions of states M and P at internal nodes on the consensus tree summarizing the tree sample. The means of the posterior probability distributions of states M and P at a given node, denoted $p(M \mid \text{node})$ and $p(P \mid \text{node})$, are multiplied by the posterior probability of the node itself, denoted $p(\text{node})$, to produce the combined probabilities of the two states at the node, denoted $p(M)$ and $p(P)$; $p(M \mid \text{node}) + p(P \mid \text{node}) = 1$, thus $p(M) + p(P) = p(\text{node})$. This means that if reconstruction of the node itself is uncertain [i.e., if $p(\text{node}) < 1$], the value of $p(\text{node})$ sets an upper limit to the confidence that can be placed in the ancestral state reconstructions for the node. As a rule of thumb, confidence can be placed in reconstructions with combined probabilities ≥ 0.70 .

The other four sets of analyses were used to assess explicitly the relative “fit” of states M and P at nodes PIH and PIE. For each node, one set of analyses was run with the node fixed (“fossilized”) to state M and one with the node fixed to state P. The posterior probability distributions of $\log_e(\text{likelihood})$ values sampled by the chains reflect how well a given fossil state fits the node; a measure called the “Bayes factor,” which is used to compare posterior probability distributions (Kass and Raftery 1995; Raftery 1996), provides an indication of the strength of the evidence in favor of one state over the other at the node. The Bayes factor for state M over state P is denoted B_{MP} . $2\log_e(B_{MP})$ is approximated as twice the difference between $\log_e[H(\text{likelihood})]$ for a chain fixed on state M and $\log_e[H(\text{likelihood})]$ for a chain fixed on state P, where $\log_e[H(\text{likelihood})]$ is the natural logarithm of the harmonic mean of the likelihood values. In theory, values of $2\log_e(B_{MP}) > 0$ represent evidence for state M and values of $2\log_e(B_{MP}) < 0$ evidence for state P. Specifically, the evidence for a given state is “weak” for $0 < |2\log_e(B_{MP})| < 2$, “positive” for $2 < |2\log_e(B_{MP})| < 5$, “strong” for $5 < |2\log_e(B_{MP})| < 10$, “very strong” for $|2\log_e(B_{MP})| > 10$ (Raftery 1996, p. 165). In practice, however, the harmonic means of likelihood values may vary across runs: they are expected to converge to the same value if the chains are run to infinity. Consequently, I take the conservative approach recommended by Pagel and Meade (n.d.), which disregards any evidence for either state given by $|2\log_e(B_{MP})| < 2$.

I determined the RJ-MCMC chain specifications through preliminary maximum-likelihood and MCMC runs, all with nodes not fossilized. These specifications ensure that the RJ-MCMC chains sample parameter space adequately and ultimately converge to the posterior probability distribution of states in the model of trait evolution. I ran the RJ-MCMC chains for 10^8 iterations, sampling every 10^3 , with an additional burn-in of 10^6 , and rate deviation set to 50. All chains used a uniform prior on the models and an exponential prior on the rate parameters; the mean of the exponential prior was seeded from a uniform hyperprior on the interval 0–10. The shape of the prior distribution (exponential or gamma) and the interval of the hyperprior (0–10 or 0–20) only marginally affected the mean of the posterior probability distributions of $\log_e(\text{likelihood})$ values and of ancestral states, returning qualitatively similar results.

For each set of analyses, convergence to the posterior probability distribution of states in the model of trait evolution was assessed by comparing the samples returned by the separate chains, through visual inspection of (i) time-series plots of $\log_e(\text{likelihood})$ values, (ii) the posterior probability distributions of model categories, and (iii) the average deviation of parameter estimates across runs. The near-independence of sampling events was judged from the autocorrelation of the $\log_e(\text{likelihood})$ values of successive states sampled by the chains. In all cases, these diagnostics indicated that the chains sampled the target distributions adequately.

Results

For each set of analyses, I compared the $\log_e[H(\text{likelihood})]$ values for the states in the model of trait evolution sampled by the separate chains at

Table 1. Summary of the Posterior Probability Distribution of Model Categories

A. Rate Classes, Frequencies, and $\log_e(\text{likelihood})$ Values

Model category	Rate Class ^a		Frequency ^b			$\log_e(\text{likelihood})$ (mean \pm SD)
	q_{MP}	q_{PM}	Absolute	Relative	Cumulative	
1	0	0	87811	0.878		-11.23 ± 0.72
2	Z	0	11481	0.993		-12.90 ± 0.92
3	0	1	614	0.999		-11.44 ± 0.84
4	0	Z	94	1.000		-17.74 ± 0.88

B. Rate Values and Ancestral States at Nodes PIH and PIE

Model category	Rate (mean \pm SD)		Node PIH		Node PIE	
	q_{MP}	q_{PM}	$p(M \text{node})$ \pm SD	$p(P \text{node})$ \pm SD	$p(M \text{node})$ \pm SD	$p(P \text{node})$ \pm SD
1	3.10 ± 2.16	3.10 ± 2.16	0.79 ± 0.11	0.21 ± 0.11	0.93 ± 0.08	0.07 ± 0.08
2	0.00 ± 0.00	5.06 ± 2.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00
3	2.60 ± 1.87	4.19 ± 3.26	0.72 ± 0.16	0.28 ± 0.16	0.84 ± 0.18	0.16 ± 0.18
4	3.71 ± 1.51	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00	1.00 ± 0.00	0.00 ± 0.00
All	2.74 ± 2.26	3.33 ± 2.24	0.70 ± 0.27	0.30 ± 0.27	0.83 ± 0.31	0.17 ± 0.31

a. "Z" denotes rates assigned to the zero class. "0" and "1" denote two distinct non-zero rate classes; rates with the same value are assigned to the same non-zero rate class. For example, under model category 1 q_{MP} and q_{PM} are assigned to the same non-zero rate class, that is, they take the same positive value; under model category 2 q_{MP} is assigned to the zero rate class, that is, it is set to zero, while q_{PM} is assigned to a non-zero rate class, that is, it takes a positive value; under model category 3 q_{MP} and q_{PM} are assigned to distinct non-zero rate classes, that is, they take different positive values.

b. The relative cumulative frequency of a model category is obtained by summing the absolute frequency of sampled points in the model category to the absolute frequencies of sampled points in all preceding categories, if any, and then dividing by the total number of sampled points in all categories [e.g. $(87,811 + 11,481)/10^5 = 0.993$ for model category 2].

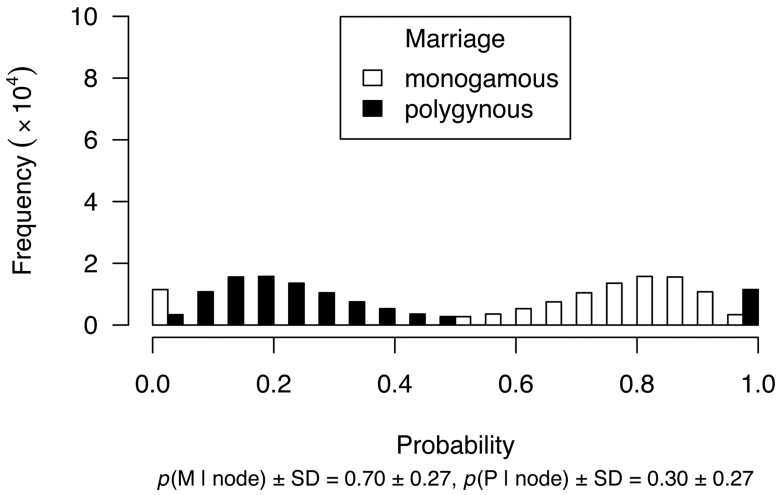


Figure 2. Posterior probability distributions of states M and P at node PIH.

convergence; I present results for the chain that returned the median value of the $\log_e[H(\text{likelihood})]$. Below I discuss the ancestral state estimation at nodes on the consensus tree. The fossilization of nodes PIH and PIE largely confirms the ancestral state estimation and is discussed in the SI file.

Estimation of Ancestral States on the Consensus Tree. At convergence, the chain sampled states in the model of trait evolution with mean $\log_e(\text{likelihood}) \pm \text{SD} = -11.43 \pm 0.93$ (range: -21.34 to -9.94 ; auto-correlation coefficient: $r = 0.003$; mean acceptance rate: 22.9%). Below I

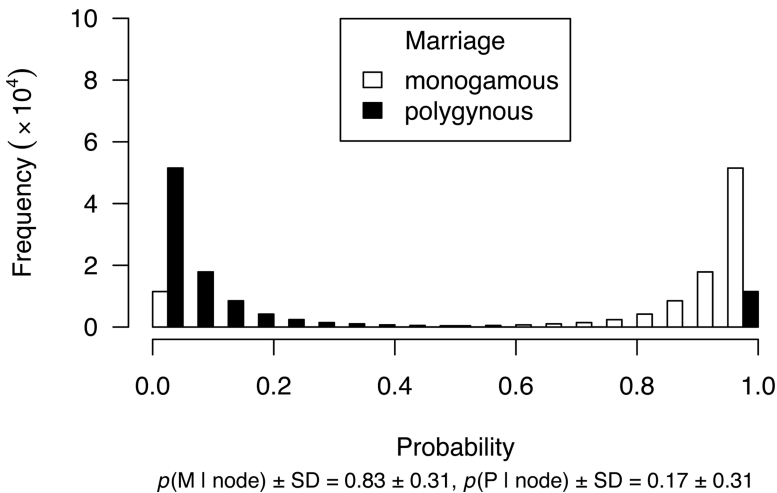


Figure 3. Posterior probability distributions of states M and P at node PIE.

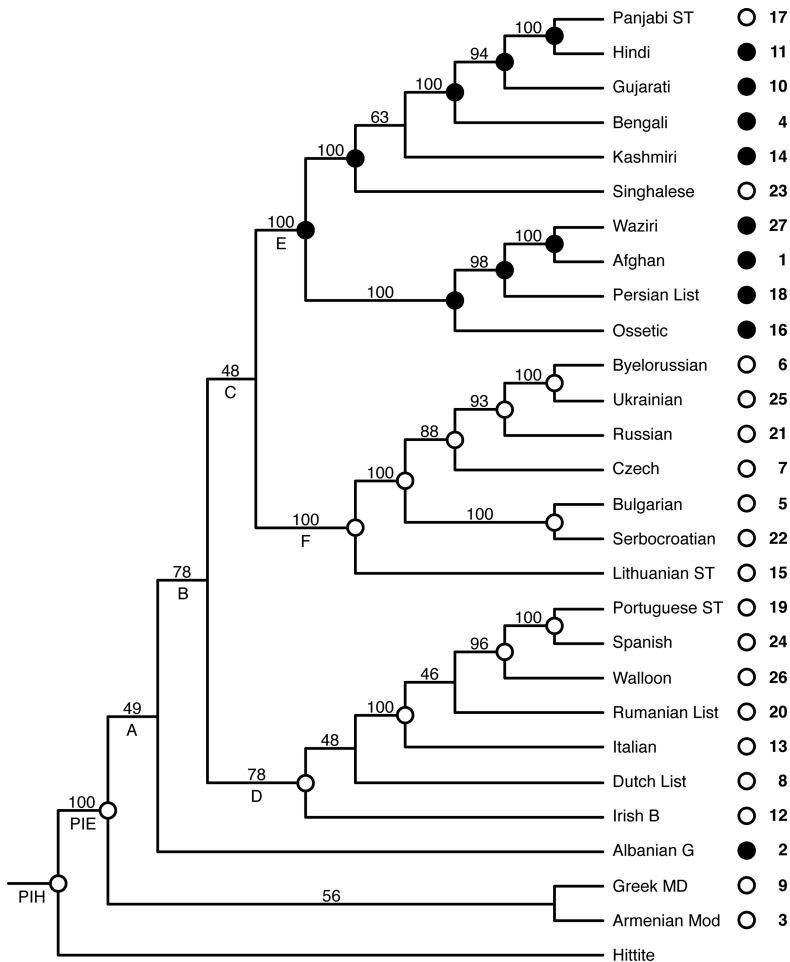


Figure 4. Majority-rule consensus tree of Pagel et al.'s (2007) sample of 750 trees for 84 IE speech varieties and three outgroups, pruned to 27 IE speech varieties plus the outgroup Hittite. The tree includes nodes present in >50% of trees in the sample, plus other compatible groupings; the value above each node represents the node's posterior probability, $p(\text{node})$, as a percentage. Numbers in bold at the tips correspond to societies in Figure 1. Tips are color-coded to represent the marriage strategy of the corresponding societies (white, M; black, P; Hittite was not assigned marriage strategy data). Nodes are color-coded to represent the combined probabilities of the two states [white, $p(M) \geq 0.70$; black, $p(P) \geq 0.70$; other nodes have combined probability <0.70 for both states].

discuss separately the posterior probability distribution of model categories returned by the chain and the ancestral state estimates over all model categories.

Posterior Probability Distribution of Model Categories. The chain sampled the four possible model categories with the frequencies reported in Table 1a: for

Table 2. Ancestral States of Marriage Strategy at Selected Nodes on the Consensus Tree

Node ^{a,b}	$p(\text{node})$	$p(M \mid \text{node}) \pm \text{SD (range)}$	$p(P \mid \text{node}) \pm \text{SD (range)}$
A	0.49	0.77 ± 0.29 (0.00–1.00)	0.23 ± 0.29 (0.00–1.00)
B	0.78	0.82 ± 0.31 (0.00–1.00)	0.18 ± 0.31 (0.00–1.00)
C	0.48	0.61 ± 0.21 (0.00–1.00)	0.39 ± 0.21 (0.00–1.00)
D	0.78	0.93 ± 0.08 (0.50–1.00)	0.07 ± 0.08 (0.00–0.50)
E	1.00	0.08 ± 0.09 (0.00–1.00)	0.92 ± 0.09 (0.00–1.00)
F	1.00	0.96 ± 0.04 (0.50–1.00)	0.04 ± 0.04 (0.00–0.50)

a. The letters correspond to the node labels in Figure 4.

b. The combined probabilities, $p(M)$ and $p(P)$, are obtained as $p(M) = p(M \mid \text{node}) \cdot p(\text{node})$ and $p(P) = p(P \mid \text{node}) \cdot p(\text{node})$.

example, q_{MP} and q_{PM} were assigned to the same rate class in 87.8% of the 10^5 sampled points (model category 1). Over the four model categories, rates were assigned to 1.01 ± 0.08 non-zero classes (mean \pm SD; range: 1–2 non-zero classes); this indicates that the evolutionary transitions that produced the observed distribution of states of marriage strategy across societies in the sample can be described by a simple model of trait evolution based on only one non-zero rate class (rate classes “0” and “1”).

Nodes PIH and PIE reconstructed as monogamy with high posterior probabilities under model categories 1, 3, and 4, and as polygyny with $p(P \mid \text{node}) = 1$ under model category 2 (Table 1b). In the latter category, transitions from monogamy to polygyny are excluded, because q_{MP} is set to zero (rate class “Z”). This forces nodes PIH and PIE to reconstruct as polygyny: under this category, any variation in states of marriage strategy at the tips of the tree is the result of transitions from polygyny to monogamy. In other words, the presence of polygyny at the tips could not be accounted for if PIH and/or PIE reconstructed as monogamy. However, models in category 2 returned a mean $\log_e(\text{likelihood})$ value 1.67 units worse than models in the category that returned the best mean $\log_e(\text{likelihood})$ value (category 1, Table 1a), and 1.47 units worse than the mean $\log_e(\text{likelihood})$ value over the four model categories. This suggests that the evolutionary scenario described by model category 2 (“deep” polygyny; no transitions from monogamy to polygyny) is unlikely to have produced the observed distribution of states of marriage strategy across societies in the sample.

Posterior Probability Distributions of Ancestral States. Over the four model categories, nodes PIH and PIE reconstructed as monogamy with high posterior probabilities (Table 1b). The posterior probability distribution is more strongly skewed toward high values for state M at node PIE, as reflected in the higher value of $p(M \mid \text{node})$ at this node (Figures 2 and 3; see discussion of the fossilization analysis in the SI file).

Monogamy reconstructed with high posterior probabilities through to nodes A and B on the consensus tree summarizing the tree sample, but

phylogenetic uncertainty limits the confidence that can be placed in these inferences (Figure 4 and Table 2). Node D (the common ancestor of societies speaking Italic, Germanic, and Celtic languages) and node F (the common ancestor of societies speaking Baltic and Slavic languages) reconstructed as monogamy with high posterior probabilities. Node E (the common ancestor of societies speaking Indian and Iranian languages) reconstructed as polygyny with high posterior probability.

The uncertainty in the reconstructions at the base of the consensus tree means that a host of scenarios can explain the distribution of states of marriage strategy at the tips (Figure 4). Polygyny was acquired at least once on the tree, between nodes PIE and E, and possibly a second time in the branch leading to Albanian G. A minimum of two reversals to monogamy occurred, one in the branch leading to Panjabi ST and one in the branch leading to Singhalese.

Discussion

The phylogenetic comparative analysis of marriage strategies across societies speaking IE languages provides evidence in support of PIE monogamy; this pattern likely extended back to PIH, but the evidence is only suggestive. Polygyny evolved at least once, possibly twice, throughout the history of IE-speaking societies, but uncertainty in some of the “deep” reconstructions means that alternative evolutionary scenarios cannot be excluded. This uncertainty emphasizes the need for an explicitly historical approach when deriving inferences about past social organization from cross-cultural data, and to cross-cultural comparison more generally. In turn, the uncertainty in the phylogenetic model used to represent how the societies are related by descent stresses the importance of avoiding “best tree” approaches in phylogenetic comparative analysis.

As discussed above, Fortunato and Mace (2009) used a “best” tree in the phylogenetic comparative analysis of marriage strategies and strategies of wealth transfer at marriage in IE-speaking societies. The present findings suggest that their reconstruction of PIH monogamy is not contingent upon the phylogenetic tree used. Further, while the outgroup Hittite was not assigned marriage strategy data in the present analysis, it was coded as monogamous in Fortunato and Mace’s (2009); this was necessary because the phylogenetic comparative method they used did not allow missing data (Pagel n.d.). The present findings indicate that the reconstruction by Fortunato and Mace (2009) is not contingent upon the state they assigned to the outgroup. Applying a phylogenetic comparative approach to the marriage transfer strategy data, in a Bayesian MCMC framework, Fortunato et al. (2006) showed that the reconstruction of PIH dowry is similarly robust to phylogenetic tree model and coding of the outgroup.

More generally, these reconstructions push the origin of monogamous marriage into prehistory, well beyond the earliest instances documented in the

historical record. This implies that the archaeological and genetic evidence for the nuclear family in prehistoric populations may reflect a monogamous marriage strategy; on their own, the archaeological and genetic data can at best provide clues about a monogamous *mating* pattern. For example, Haak et al. (2008) found evidence, through analysis of aDNA samples, of genetic relatedness of one adult male and one adult female with two children recovered in one burial at the site of Eulau, Germany, a late Neolithic community (c. 2600 BCE) attributed to the Corded Ware culture; they argued that this establishes “the presence of the classic nuclear family in a prehistoric context in Central Europe” (Haak et al. 2008, p. 18,229). Similarly, Bentley et al. (2008) identified a nuclear family, comprising an adult male, an adult female, a mature female, and two children, through analysis of the isotopic signatures of skeletal remains in the communal grave at Talheim, Germany, an early Neolithic community (c. 4900–4800 BCE) attributed to the Linear Ware culture; previous analysis of the teeth had revealed high similarity between the male and the children, suggestive of genetic relatedness. The Corded Ware and Linear Ware cultures are archaeological horizons of northern and central Europe associated with populations speaking IE languages (Mallory 1997a,b). The phylogenetic comparative analysis shows that monogamous marriage prevailed among prehistorical IE-speaking societies located in Europe. At least to the extent that evidence from a single grave can substantiate claims such as Haak et al.’s (2008), this suggests that the burial patterns may reflect the monogamous marriage strategy of the Eulau and Talheim communities.

Larger-scale analyses of Y-chromosome data provided evidence for a later increase in effective male population size compared to effective female population size, across European (Dupanloup et al. 2003; Pereira et al. 2001) and worldwide (Dupanloup et al. 2003) samples. One possible interpretation of this pattern is that the difference in effective population size was caused by a regime of polygynous mating, which resulted in greater variance in reproductive success for males than for females (Dupanloup et al. 2003; Pereira et al. 2001). Further, Dupanloup et al. (2003) interpreted the delayed increase in the effective male population as evidence for a relatively recent shift from polygynous to monogamous mating; based on Pritchard et al.’s (1999) estimates for the timing of expansion of Y-chromosome data, they linked this shift to the emergence of food production, between 10,000 and 5000 years ago in Europe and Asia and more recently elsewhere, when “Nuclear families replaced the polygamous, extended-family compounds typical of hunting-gathering populations” (Dupanloup et al. 2003, p. 96). Dupanloup et al. (2003) use the concept of “nuclear family” as synonymous with non-extended and monogamous family organization, although in anthropology it is used to designate a family unit comprising parents and their dependent children (Fox 1983, p. 36; Keesing 1975, p. 150; Parkin 1997, p. 28); technically, therefore, nuclear families exist in societies practicing monogamous and polygamous marriage (Murdock 1949, pp. 1–2; see discussion in Fox 1983, pp. 36–40). The reconstruction of PIE monogamy presented in this paper, with

monogamy likely extending back to PIH, falls within the temporal interval identified by Dupanloup et al. (2003), suggesting that monogamous marriage had emerged in Eurasia by that time. However, Dupanloup et al.'s (2003) interpretation holds only to the extent that the shift to the "nuclear family" (i.e., from polygynous to monogamous marriage, based on their usage of the concept) coincided with a shift from polygynous to monogamous mating, with consequent reduction in the variance in male reproductive success. The historical and ethnographic evidence suggest that variance in male reproductive success is comparable in societies practicing monogamous and polygynous marriage (Fortunato and Archetti 2010). In any case, this pattern is to be viewed against the background of moderately polygynous mating that is believed to have characterized our species' evolutionary past based on morphological (e.g., Alexander et al. 1979; Harcourt et al. 1981) and genetic (e.g., Hammer et al. 2008; Labuda et al. 2010) data.

Finally, and most importantly, the phylogenetic comparative analysis confutes explanations linking the emergence of monogamous marriage to the development of features of social organization typically associated with the "complex," "modern" societies located in Eurasia. Indeed, investigation of the factors resulting in the shifts from monogamy to polygyny identified by the phylogenetic comparative analysis, and in the corresponding reversals, would be of particular interest. Shifts in marriage strategies may reflect, for example, changes in subsistence systems, as well as historical contingencies such as the diffusion of religious beliefs (e.g., Fortunato and Archetti 2010; Goody 1983). Recent theoretical work situates variation in marriage strategies in the context of variation in ecological factors, linking the prevalence of monogamy across Eurasian societies to the development of intensive modes of production (Fortunato and Archetti 2010). Diamond (1998) has convincingly argued that the relative greater "complexity" of these societies, and their consequent "modernization," can also be attributed to ecological determinants that facilitated the emergence of food production in the region. This raises the possibility that ecological factors act as a confounding variable in the observed relationship between marriage strategies and indicators of "societal complexity" and "modernization." An appeal to "complexity" and "modernization" as the terminus of explanation amounts to providing a proximate answer to ultimate questions about the evolution of marriage strategies.

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